

## Residency effects on territoriality in the butterfly *Chrysozephyrus smaragdinus* (Lepidoptera: Lycaenidae)

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**Abstract** I performed field observations on the lycaenid butterfly, *Chrysozephyrus smaragdinus* Bremer (Lepidoptera: Lycaenidae) to estimate the payoff of their territorial activity. The owners defended their territories through several contests per day. During their territorial activity, owners did not visit flowers or tree saps and they did not mudpuddle, which is congruent with the previous finding that territory-owners among *C. smaragdinus* had less fat than intruders. They seem not to recover energy during their territorial activity. I also reexamined the relationship between male arrival order and their territorial status, which was shown by a previous study. Males arriving early at territory sites in the adult season tended to subsequently hold these sites irrespective of their body size. Thus the reproducibility of the previous study was confirmed. The present study revealed that residency effects are the basic characteristics of the territoriality of this species.

**Key words** arrival order, contest, protandry, territory.

## Introduction

Males of various butterfly species defend mating territories through aerial contests (Kemp and Wiklund, 2001; Kemp, 2013). In violent contests, which are usual in most animals, physical abilities are often correlated with contest success (Hardy and Briffa, 2013). However, butterflies do not have organs such as teeth, nails or horns with which to attack their opponent, and their contests are generally non-contact aerial interactions. The characteristics correlated to territorial dominance are not obvious in butterflies, and revealing the factors determining dominance in such animals is an exciting theme in ethology.

*Chrysozephyrus smaragdinus* Bremer (Lepidoptera: Lycaenidae) is a territorial butterfly distributed in East Asia (Koiwaya, 2007). Takeuchi and Imafuku (2005) conducted detailed observations of territorial behavior of *C. smaragdinus*. Males monopolize a space surrounded by trees as their mating territory, where no resources such as flowers or oviposition sites are present. Males compete for the sites through conspicuous aerial interactions, flying around each other until one of them retreats. Some males were apparently owners of territory because they occupied it for an average of 9 days (up to 28 days), winning a lot of contests, while other males were not. To investigate why the owners can dominate

non-owners, Takeuchi and Honda (2009) performed behavioral experiments and showed that males which had occupied the contested territory longer win contests over the territory. This is a kind of residency effect, which is widespread in the animal kingdom (Kokko *et al.*, 2006). This result predicts a population-level territorial dynamics. Since residency period per se confers advantages in their territorial contests, males arriving at a territory early in their adult season would acquire territorial dominance because they can remain there for a certain period with only a few rivals; late-appearing males do not have this advantage. As predicted, Takeuchi and Honda (2009) found that males appearing at territory sites early in the reproductive season were more likely to hold their territories, irrespective of their body size. The advantages of early comers in territorial dominance are well known in migratory birds (Sergio *et al.*, 2007 and see review in). In insects, however, this phenomenon is only known in *C. smaragdinus*.

Of course, residency effects would be a matter of degree. In cases where there are too many contests over their territory, owners would use up their flight energy and could not continue defending their territory. In fact, territory-owners among *C. smaragdinus* had less fat than intruders, suggesting that owners lost their energy reserve through their territorial activity (Takeuchi, 2006a). They

may have to leave their territory to obtain food such as nectar.

In the present study, I observed territorial behavior by *C. smaragdinus* males in Nagano city. The study site was much smaller than the study site used by Takeuchi and Honda (2009), and therefore I could watch almost all behaviors of territory owners. To estimate the payoff of territorial activity, I counted the number of contests territory owners performed and how many times territory owners went to feed. I also counted the number of matings achieved by territory owners. In addition, I reexamined whether males of *C. smaragdinus* which arrived at territory sites earlier in the adult season had advantages in holding their territories.

## Materials and methods

### Study sites and periods

The study area was located in Nagano City (36°39'N, 138°10'E, 400 m alt), Nagano Prefecture, Japan. The area was an artificial gap (approximately 30 m × 10 m) in a temperate deciduous forest (Fig. 1). In this area the males of *C. smaragdinus* exhibited territorial behavior between mid June and early July (univoltine). The butterflies were observed on leaves of limbs around the edges of the forest facing the gap (Fig. 2). As is often the case with studies on forest butterflies, the observable area was rather small and the number of males observed was limited. However, that enabled me to survey all territories and to confirm when each male arrived in the area. I performed observations in June 2002, before the butterflies emerged, until the day when the number of identified males exceeded 10 (the eleventh male day).

### Observation

I surveyed the study area daily between 0900 and 1700. This time period covered the daily territorial activity of *C. smaragdinus* (Takeuchi and Imafuku, 2005). I captured males when they first appeared in the study area. They were immediately individually marked with water-insoluble ink along the edges of the ventral surface of both wings and released on the spot. Forewing length was measured to the nearest 0.1 mm with vernier calipers. By this means I was able to establish the date of arrival at the study area for each male. I recorded the ID of males that occupied each territory site on an hourly basis. If a sole male occupied a territory site within a daily activity period, I considered that the male was the owner of the territory on that day. If two or more males occupied a territory site one after another within a daily activity period, I considered the males were not owners but temporally perching individuals on that day.

I observed the territory-owners throughout the daily territorial activity between 13 and 15 June. I recorded the number of contests and matings each owner performed and whether each owner visited food sources during its territorial activity.

### Data analyses

To evaluate the territorial dominance of males, appropriately categorizing the males as dominant or subordinate individuals is important. It should be noticed that any male is expected to hold a territory without difficulty at the beginning of the adult season irrespective of his traits because only a few rivals exist at this stage. Therefore, the territorial status of males should be judged based on whether a male could hold a territory when the number of rivals increased. I classified the status of each male into 2 categories: (1) dominant: if he was an owner on the eleventh male day and (2) subordinate: if he was a temporally perching individual or not recorded at any territory site on the eleventh male day.

Differences in mean values of arrival date and body size (forewing length) between dominant and subordinate individuals were tested with Wilcoxon rank sum test. Spearman correlation coefficients between arrival date and forewing length are also calculated and tested. I used R 2.15.0 (R Development Core Team, 2012) for all statistical tests.

## Results

*Chrysozephyrus smaragdinus* was first observed in the adult season on 9 June, and then the number of males gradually increased thereafter (Fig. 3). The eleventh male day was 15 June (Fig. 3). There are three major territories in the study area (Fig. 4). Male 1 occupied the central territory, and male 2 occupied the right one (Fig. 4).

Forewing length did not differ between dominant and subordinate individuals (dominant  $20.4 \pm 2.05$  mm,  $N = 2$ ; subordinate  $22.1 \pm 0.434$  mm,  $N = 9$ ,  $W = 1.5$ ,  $P = 0.095$ ).

Two or three owners were found on each day (Fig. 3). They defended their territory between *ca.* 1000 and 1600. The number of contests each owner performed is shown in Table 1. On 14 June, two contests between the owners of two neighboring territories (male1 and male2) occurred. Both males returned to their own territory after the contests. I never observed mating behavior nor did I ever observe that territory owners fed during their territorial activity. The correlation between forewing length and arrival date was not significant ( $r = 0.57$ ,  $t = 2.07$ ,  $d.f. = 9$ ,  $P = 0.068$ ).



Fig. 1. The study site. Nagano City, Nagano Pref., Japan.



Fig. 2. A territorial male of *C. smaragdinus*.

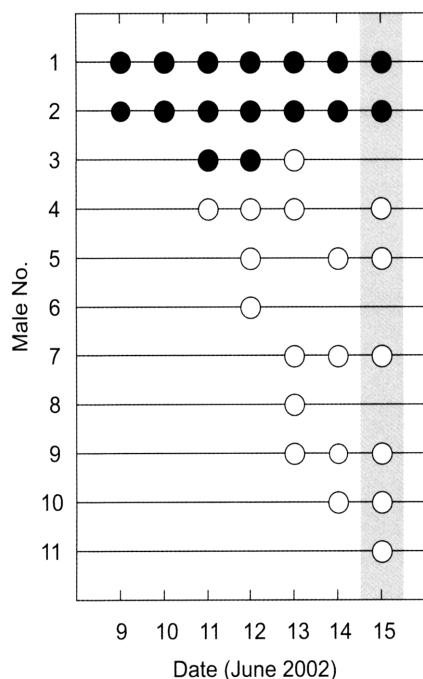


Fig. 3. Territorial status of each male on each day. Filled circle indicates that he was a territory owner. Open circle indicates that he was not an owner but was found in the study area. No circle indicates that he was not found in the study area. Male No. corresponds to his arrival order. Grey band indicates the eleventh male day.

Arrival date differed between dominant and subordinate individuals ( $W = 0$ ,  $N_{dom} = 2$ ;  $N_{sub} = 9$ ,  $P = 0.036$ ). Dominant individuals arrived at the area earlier than subordinate individuals. Both the dominant individuals arrived at the territory sites on the first day of the adult season, and occupied the sites from then on (Fig. 3).

## Discussion

The owners defended their territories through several contests per day. Owners never fed during their territorial activity. Although they might eat something on leaves they perched on during their territorial activity, at least I did not observe that they visited flowers or tree saps or that they mudpuddled. They seemed not to recover energy during their territorial activity, which is congruent with the previous finding that owners of *C. smaragdinus* had less fat than intruders (Takeuchi, 2006a). When do they eat something? At the end of the territorial activity (16:37), a territorial male visited flowers of *Hydrangea paniculata* in Shiojiri, Nagano Pref. on 16 June 2001 (Takeuchi *Pers. Obs.*).

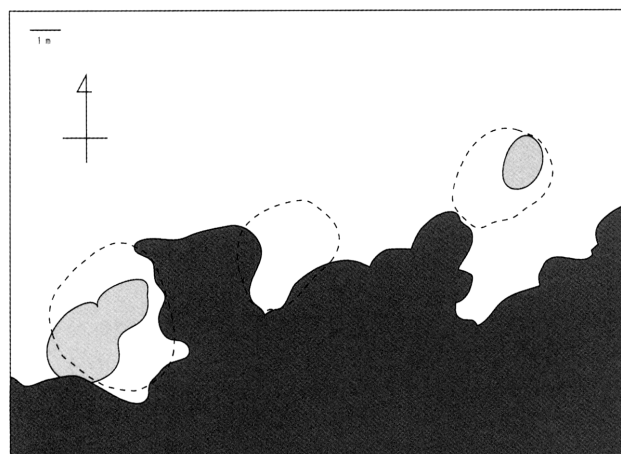


Fig. 4. A map of the territories of *Chrozophyrus smaragdinus*. Dark gray; tall trees, Light gray; short trees, White; pasture, dashed lines; defended area (territories).

Table 1. The number of contests each owner engaged in.

	13-Jun	14-Jun	15-Jun
male 1	7	2	2
male 2	2	7	3

I never observed mating behavior. Part of the reason might be that females did not emerge during the study periods. I observed *C. smaragdinus* during the first 7 days of their adult season. Males emerge earlier than females in many butterfly species, which is known as protandry (Gotthard, 2008). However, even in the middle of their adult season, mating behavior of *C. smaragdinus* has rarely been observed (Takeuchi and Honda, 2009). Imafuku (2008) showed that females of this species mate only once. If the sex ratio is 1:1, a male is expected to mate once during its lifetime, which may make observation of mating difficult.

Forewing length was not correlated with territorial status of the males. Previous studies also showed that body size was not correlated with contest success in this butterfly (Takeuchi, 2006a, b; Takeuchi and Honda, 2009). A lack of relationship between body size and contest success has been reported in various butterflies (Lederhouse, 1982; Kemp, 2000; Kemp, 2003; Kemp *et al.*, 2006). In addition, the relationship between body size and arrival date was not significant, and therefore there is no

evidence that males that appear at a territory site early have experienced better nutritional conditions during their larval periods. Rather, later arriving males tend to be larger: the correlation between arrival date and forewing length was positive ( $r = 0.57$ ). This may mean that longer larval periods were required to become larger adults (Teder, 2014).

Males of *C. smaragdinus* that arrived at territory sites early in the adult season remained territory-owners even when the number of males increased. In fact, both the dominant males arrived on the first day of the adult season (Fig. 3). A negative relationship between arrival date and territorial status in *C. smaragdinus* was also observed in Matsumoto, Nagano Pref. Japan (Takeuchi and Honda, 2009), and therefore its reproducibility was confirmed in the present study. This is important because ecological phenomena are sometimes not reproducible. For instance, Davies (1978) showed in Wytham Woods in England that territorial contests of the speckled wood butterfly *Pararge aegeria* were resolved based on a bourgeois strategy: the resident always wins (Maynard Smith, 1982). However, the contrary phenomenon was observed in Ågesta in Sweden (Wickman and Wiklund, 1983), and in an experimental cage (Kemp and Wiklund, 2004). One of the reasons why ecological phenomena are sometimes not reproducible would be that ecological phenomena are often subject to environmental factors that are difficult to control. Since a series of studies on territorial behavior of *C. smaragdinus* found residency effects in their contests (Takeuchi, 2006b; Takeuchi and Honda, 2009) and in their territorial dynamics (Takeuchi and Honda, 2009; Takeuchi *in press*), the effects would be basic characteristics of the territoriality of this species.

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## References

- Davies, N. B., 1978. Territorial defence in the speckled wood butterfly (*Pararge aegeria*): the resident always wins. *Anim. Behav.* **26**: 138-147.
- Gotthard, K., 2008. Adaptive growth decisions in butterflies. *Bioscience* **58**: 222-230.
- Hardy, I. C. W and M. Briffa, 2013. *Animal contests*, Cambridge University Press, Cambridge.
- Imafuku, M., (2008) Variation in number of copulations in Theclini butterfly females (Lycaenidae: Lepidoptera). *Entomol. Sci.* **14**: 142-146.
- Kemp, D. J., 2000. Contest behavior in territorial male butterflies: does size matter? *Behav. Ecol.* **11**: 591-596.
- Kemp, D. J., 2003. Twilight fighting in the evening brown butterfly, *Melanitis leda* (L.) (Nymphalidae): age and residency effects. *Behav. Ecol. Sociobiol.* **54**: 7-13.
- Kemp, D. J., 2013. Contest behaviour in butterflies: fighting without weapons. In Hardy I. C. W and M. Briffa (eds) *Animal contests*, pp. 134-146. Cambridge University Press, Cambridge.
- Kemp, D. J. and C. Wiklund, 2001. Fighting without weaponry: a review of male-male contest competition in butterflies. *Behav. Ecol. Sociobiol.* **49**: 429-442.
- Kemp, D. J. and C. Wiklund, 2004. Residency effects in animal contests. *Proc. R. Soc. Lond. B* **271**: 1707-1711.
- Kemp, D. J., C. Wiklund and H. Van Dyck, 2006. Contest behaviour in the speckled wood butterfly (*Pararge aegeria*): seasonal phenotypic plasticity and the functional significance of flight performance. *Behav. Ecol. Sociobiol.* **59**: 403-411.
- Koiwaya, S., 2007. The zephyrus hairstreaks of the world. Mushisha, Tokyo. (In Japanese)
- Kokko, H., A. López-Sepulcre and L. J. Morrell, 2006. From hawks and doves to self-consistent games of territorial behavior. *Am. Nat.* **167**: 901-912.
- Lederhouse, R. C., 1982. Territorial defense and lek behavior of the black swallowtail butterfly, *Papilio polyxenes*. *Behav. Ecol. Sociobiol.* **10**: 109-118.
- Maynard Smith, J., 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge.
- R Development Core Team., 2012. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>
- Sergio, F., J. Blas, M. G. Forero, J. A. Donazar and F. Hiraldo, 2007. Sequential settlement and site dependence in a migratory raptor. *Behav. Ecol.* **18**: 811-821.
- Takeuchi, T., 2006a. The effect of morphology and physiology on butterfly territoriality. *Behaviour* **143**: 393-403.
- Takeuchi, T., 2006b. Matter of size or matter of residency experience? Territorial contest in a green hairstreak, *Chrysozephyrus smaragdinus* (Lepidoptera: Lycaenidae). *Ethology* **112**: 293-299.
- Takeuchi, T., *in press*. Early comers occupy popular territories in a lycaenid butterfly, *Chrysozephyrus smaragdinus* (Lepidoptera: Lycaenidae). *Entomol. Sci.*
- Takeuchi, T. and M. Imafuku, 2005. Territorial behavior of a green hairstreak *Chrysozephyrus smaragdinus* (Lepidoptera: Lycaenidae): site tenacity and wars of attrition. *Zool. Sci.* **22**: 989-994.
- Takeuchi, T. and K. Honda, 2009. Early comers become owners: effect of residency experience on territorial contest dynamics in a lycaenid butterfly. *Ethology* **115**: 767-773.
- Teder, T., 2014. Sexual size dimorphism requires a corresponding sex difference in development time: a meta-analysis in insects. *Func. Ecol.* **28**: 479-486.
- Wickman, P. O. and C. Wiklund, 1983. Territorial defense and its seasonal decline in the speckled wood butterfly (*Pararge aegeria*). *Anim. Behav.* **31**: 1206-1216.

## 摘 要

メスアカミドリシジミ *Chrysozephyrus smaragdinus* の縄張り制における先住効果 (竹内 剛)

メスアカミドリシジミ *Chrysozephyrus smaragdinus* の縄張り制について過去に行われた研究では、強い先住効果が示されている。しかし、チョウの縄張り内には餌がないことが多く、縄張り争いのために過度のエネルギーを消費すれば、縄張りを離れて採餌しなければならないかもしれない。雄がどの程度縄張りを占有し続けられるかを明らかにするために、長野県長野市でメスアカミドリシジミの縄張り保持雄を3日間終日観察した。縄張り活動は10時から16時頃まで見られた。この3日間で2頭の雄がそれぞれ10回以上の闘争に勝って縄張りを占有し続けたが、縄張り活動中には一度も摂食は確認されなかつ

た。縄張り保持雄は侵入者に比べて脂肪貯蔵量が少ないことが過去に報告されているが、この結果はその事実と合致する。なお、この期間に配偶行動は見られなかった。

また、本研究では繁殖期の初めからメスアカミドリシジミの配偶縄張りを1時間ごとに観察し、雄が現れたら直ちに個体識別した。最初の雄が現れてから6日後に、個体識別された雄が11頭に達した。この時点でどの個体が縄張りを保持していたかを調べたところ、過去の研究と同じく、繁殖期の初めに配偶縄張りに現れた雄ほど、その後も縄張りを保持している確率が高かった。本研究で再現性が確認されたことから、この現象は安定して見られると考えられる。即ち、先住効果は本種の縄張り性における基本的な性質である。

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